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MITOTIC CHROMOSOME STUDIES IN THE GENUS ASTRAGALUS[1]

S. Conrade Head

The genus *Astragalus* L., tribe Galegeae of the Leguminosae, consists of about 1,500 species occurring in northern Africa, Europe, northern and central Asia, and in the western hemisphere. Some sixty genera have been proposed as segregates from it, and several taxonomic revisions of the genus or parts of it for North America, based on morphological characters, have been presented (Jones, 1923; Rydberg, 1929; Barneby, 1945, 1947, 1949, 1956). Of these, the more conservative treatments of Jones and Barneby have been found more practical for the purposes of this study.

Very little, however, is known about the cytology of this genus. According to Senn (1938), "Only two per cent of the species of the huge genus *Astragalus* have been studied. These species are based on an 8 series with

[1] This paper represents a portion of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Botany at the State College of Washington, Pullman. 1955.

two exceptions in which n=14. There are 16 diploids, 1 tetraploid, 2 hexaploids, and 1 octaploid. Considering that the species studied come from widely separated regions scattered over Europe and Asia, this is a remarkable consistency of chromosome number." According to Tischler (1938), the findings of ten workers for forty-four Old World species and four New World species were: 2n=16, thirty-three species; 2n=32, three species; 2n=48, four species; 2n=64, five species; 2n=28, 36 and 96, one species each. Vilkomerson (1943) made a survey of twenty-six species from western United States and found that for eleven 2n=24, for thirteen 2n=22, whereas the other two had 2n numbers of 16 and 44 respectively. James (1951) gave chromosome counts for three species, one each of 2n=22, 24 and 26. These several surveys account for approximately one hundred species of *Astragalus*. Certainly the consistent chromosome number stressed by Senn no longer holds. It was with the thought of adding to the chromosomal information for this genus that the present investigation was undertaken.

The author wishes to express his appreciation to Dr. Adolph Hecht, who served as advisor during the course of the research and who with Dr. Marion Ownbey kindly offered many suggestions during the preparation of the manuscript. Mr. Robert C. Barneby provided several of the collections reported here and checked many of the determinations. Mr. Ralph D. Amen offered many valuable suggestions concerning cytological methods.

Methods

The *Astragalus* collections studied are listed by species in Table 1. The source of the collection, the chromosome number, and the figure number (for those collections illustrated) are given. Voucher specimens are filed in the Herbarium of the State College of Washington.

The plants were grown in the greenhouse and later transplanted to an experimental garden at Pullman, Washington. Seeds had to be scarified either by filing or by use of concentrated sulfuric acid, with treatment in the acid from forty-five minutes to one hour being most satisfactory. The scarified seeds were placed on wet filter papers in Petri dishes until the primary root had reached a length of about fifteen mm.; the root was then removed and placed in Belling's "metaphase" modification of Navashin's solution. Root tips were also obtained from pot-bound plants. Some plants were transplanted from their natural habitat to the greenhouse and later to the garden. Since most persons preparing herbarium specimens rarely collect mature fruits, herbarium sheets did not prove to be a profitable source of seed. A few seeds were obtained from herbarium sheets, however, and those as old as nine years germinated without great difficulty provided they were mature when collected.

Paraffin sections cut at twelve microns as recommended by Senn were prepared and stained by the crystal violet-iodine method. These preparations were not as satisfactory as those obtained by a method worked out

by Amen (unpublished).[2] This method provides excellent permanent slides with the cells separated from each other. One has little difficulty in viewing separated cells under the microscope, and the observer is certain that the cells are uncut. Amen plans to publish his method in detail. My modification of his procedure is as follows:

Fix cut root tips in Belling's "metaphase" modification of Navashin's solution preferably for at least two days; remove, rinse several minutes in tap water, blot off excess water; place on slide in one drop of Haupt's adhesive; cut apical 2 mm. into several pieces and squash, using flat side of scalpel; air dry slide about 15 minutes; stain in 1 per cent methyl violet for 10 minutes, wipe off excess stain and nearly air dry; wash momentarily and again nearly air dry; place in solution of 8 grams of picric acid powder dissolved in 1 liter of 95 per cent alcohol for about 20 seconds; blot excess 1 to 2 seconds, place in absolute alcohol about 20 seconds; clear in 50 parts absolute alcohol, 25 parts xylene, and 25 parts clove oil for 3–7 minutes; pass through 2 changes of xylene; mount in piccolyte.

Slides were examined and camera lucida drawings were made of the metaphase plates using a Zeiss microscope with an apochromatic oil-immersion lens of N. A. 1.30 and an initial magnification of 2,250 times. The figure were drawn at approximately 4,350 times and reduced to 1,450 times in reproduction.

Table 1. Chromosome Numbers of Astragalus Collections Studied

Species	Chromosome Number (2n)	Figure Number	Source
Section Homalobi[3]			
A. stenophyllus T. & G.	24	1	Oregon, Morrow County: 12.9 miles southwest of Heppner, *Head 598.*
	24	2	Oregon, Baker County: 12.5 miles southeast of Baker on the Ebell Creek Road, *Head 609.*
	24	3	Oregon, Wheeler County: 16 miles south of Condon, *Head 600.*
Section Inflati			
A. lentiginosus Dougl. ex Hook. var. *lentiginosus*	22	4	Oregon, Baker County: 1 mile east of Quartz, *Head 607.*
A. cusickii A. Gray	22	5	Washington, Asotin County: near the Grande Ronde River bridge, *Head 569.*
	22, 44*[4]	36	Oregon, Baker County: 13 miles west of Richland, *Head 611.*

[2] Amen, Ralph D., former graduate student, State College of Washington. Present address: 2426 South University, Denver, Colorado.

[3] Sections are those listed by Jones (1923) although this arrangement is not always satisfactory.

[4] Diploid and tetraploid cells occur in the same root tip of many Leguminosae. See discussion on polysomaty. Such counts are indicated by an asterisk.

Species	Chromosome Number (2n)	Figure Number	Source
A. beckwithii T. & G. var. *weiserensis* M. E. Jones	22	6	Idaho, Owyhee County: 10 miles north of Silver City, on road to Murphy, *Christ 19537.*
A. allochrous A. Gray	22	7	New Mexico, Grant County: San Lorenzo, *Barneby 11172.*
Section Collini			
A. collinus (Dougl. ex Hook.) G. Don var. *collinus*	24, 48*	8, 37	Washington, Asotin County: 5.5 miles northeast of Anatone, *Head 585.*
	24	9	Washington, Asotin County: 6.3 miles northeast of Anatone, *Head 588.*
var. *laurentii* (Rydb.) Barneby	24	10	Oregon, Morrow County: 18.6 miles east of Heppner, *Head 596.*
Section Hamosi			
A. andersonii A. Gray	24	11	Nevada, Washoe County: 6 miles northwest of Univ. of Nevada Campus, Reno, *Ownbey 2925.*
A. arthurii M. E. Jones	24	12	Washington, Asotin County: 3.4 miles northeast of Anatone, *Head 587.*
A. congdonii S. Wats.	26, 52*	13, 39	California, Fresno County: Piedra, *Barneby 11417.*
Section Podo-Sclerocarpi			
A. sclerocarpus A. Gray	22	14	Washington, Benton County: 2 miles west of Enterprise (West Richland), *Head 525.*
A. pachypus Greene	22	15	California, Kern County: Caliente, *Barneby 11370.*
Section Reventi-arrecti			
A. arrectus A. Gray	24	16	Washington, Whitman County: Prairie Strip, Botany Dept. State College of Washington, Pullman, *Head 584.*
A. sheldonii (Rydb.) Barneby	24	17	Washington, Asotin County: 3.4 miles northeast of Anatone, *Head 586.*
A. riparius Barneby	24	18	Washington, Whitman County: 3.3 miles northeast of Wawawai, *Head 562.*

Species	Chromosome Number (2n)	Figure Number	Source
	24	19	Washington, Whitman County: 1.1 miles east of Wawawai, *Head 563.*
A. conjunctus S. Wats.	24	20	Oregon, Wheeler County: 16 miles south of Condon, *Head 599.*
A. eremeticus Sheldon var. *malheurensis* (Heller) Barneby	24	21	Idaho, Washington County: just north of Weiser, *Ownbey 2761.*
Section Uliginosi			
A. canadensis L. var. *mortonii* (Nutt.) S. Wats.	16	22	Washington, Whitman County: north slope of Kamiak Butte, *Head 613.*
Section Chaetodontes			
A. spaldingii A. Gray	24	23	Washington, Whitman County: ½ mile east of Lacrosse, *Head 582.*
Section Argophylli			
A. inflexus Dougl. ex Hook.	22	24	Washington, Whitman County: 1 mile northeast of Wawawai, *Head 499.*
A. purshii Dougl. ex Hook. var. *glareosus* (Dougl. ex Hook.) Barneby	22, 44*	25, 38	Oregon, Baker County: 1 mile east of Quartz, *Head 547.*
	22	26	Oregon, Morrow County: 18.6 miles east of Heppner, *Head 595.*
	22	27	Oregon, Grant County: 2.5 miles north of Mt. Vernon, *Head 603.*
	22	28	Oregon, Grant County: 2.4 miles north of Mt. Vernon, *Head 604.*
var. *purshii*	22	29	Washington, Whitman County: top of Steptoe Butte, *Head 580.*
A. chamaeleuce A. Gray	22	30	Colorado, Mesa County: 3 miles south of Fruita, *Weber 3782.*

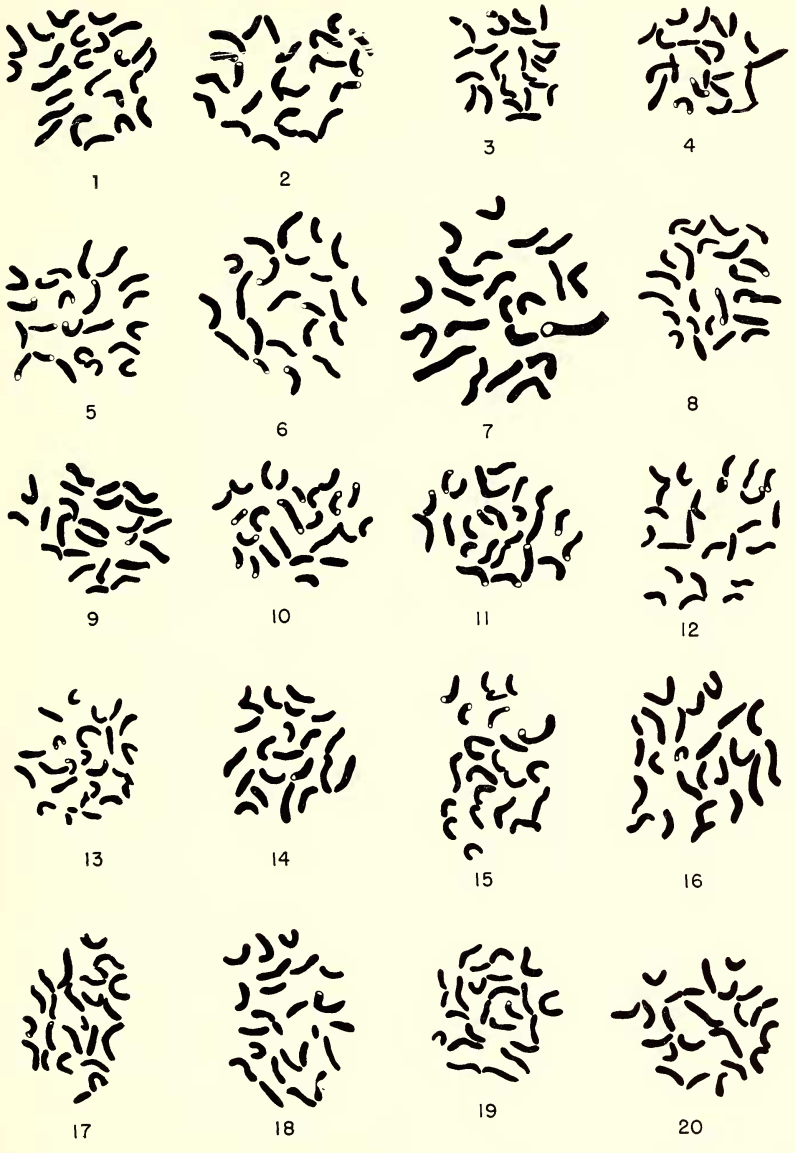
Species	Chromosome Number (2n)	Figure Number	Source
A. cibarius Sheldon	22	31	Idaho, Bannock County: 12 miles south of Portneuf, *Christ 19933.*
Section Malaci			
A. succumbens Dougl. ex Hook.	24	32	Washington, Walla Walla County: 7.4 miles east of Wallula, *Head 539.*
Section Mollissimi			
A. mollissimus Torr. var. *earlei* (Rydb.) Tidest.	24	33	Texas, Jeff Davis County: southeast of Fort Davis, *Barneby 11129.*
Section Sarcocarpi			
A. gypsodes Barneby	24	35	New Mexico, Eddy County: southwest of Whites City, *Barneby 11138.*
Section undetermined			
A. diaphanus Dougl. ex Hook.	28	34	Oregon, Wheeler County: 2 miles east of Service Creek, *Hitchcock 19235.*

Discussion

As the table indicates, chromosome numbers of 2n=16, 22, 24, 26, and 28 were found in the plants studied. The sections *Inflati, Collini, Podo-sclerocarpi, Reventi-arrecti* and *Argophylli* showed constant chromosome numbers. The section *Hamosi* had two different chromosome numbers represented; *A. andersonii* and *A. arthurii* both had 2n=24, and *A. congdonii,* 2n=26. A like situation was reported by Vilkomerson (1943) for the section *Galegiformes.* Even prior to her publication, the need for a taxonomic revision considering physiological evidence was suggested by Trelease (1942). Vilkomerson also reported a chromosome number of 2n=22 for *A. crassicarpus* Nutt.; *A. gypsodes* is recorded above as having 2n=24. Barneby (1956) groups these two species together in the same section. James (1951) found three different chromosome numbers represented by three species in the section *Didymocarpi.* Thus we see it is possible for a section to have species with different chromosome numbers. Yet, as cytological information accumulates for the genus, more sections are found to have a constant chromosome number. Much more study is needed in the section *Hamosi* and, as Trelease mentioned, in the *Galegiformes.*

Certain species of *Astragalus* can be readily identified by their characteristically shaped chromosomes. Among these are *A. succumbens* with a pair of large "question mark" chromosomes and *A. mollissimus* var. *earlei*

with its eight pairs of "C" chromosomes. The sections *Reventi-arrecti* and *Argophylli* may also be recognized by chromosome similarities of the included species.



FIGS. 1–20. Chromosomes of *Astragalus*. 1–3, *A. stenophyllus*; 4, *A. lentiginosus* var. *lentiginosus*; 5, *A. cusickii*; 6, *A. beckwithii* var. *weiserensis*; 7, *A. allochrous*; 8–9, *A. collinus* var. *collinus*; 10, *A. collinus* var. *laurentii*; 11, *A. andersonii*; 12, *A. arthurii*; 13, *A. congdonii*; 14, *A. sclerocarpus*; 15, *A. pachypus*; 16, *A. arrectus*; 17, *A. sheldonii*; 18–19, *A. riparius*; 20, *A. conjunctus*. Camera lucida drawings, × 1450.

Section Homalobi (figs. 1–3, idiograms 1–3).—Geographical distribution of *A. stenophyllus* appears to have little correlation with chromosome morphology in this species. Figures 2 and 3 are from plants which grew about two hundred miles apart, yet the chromosomes appear more alike than those of figures 1 and 3 which are from plants separated by only a few miles.

Section Inflati (figs. 4–7, 37; idiograms 4–7).—In all of the *Inflati* so far studied the 2n number is 22, provided *A. diaphanus* is not referred here. However, the section as a whole cannot be characterized or identified on the basis of chromosome similarity, for the positions of the centromeres are not as consistent as in those groups already mentioned. Both *A. allochrous* and *A. cusickii* have four pairs of chromosomes with nearly median centromeres which take a characteristic "C" shape. *A. beckwithii* var. *weiserensis* has but one pair of these chromosomes. *Astragalus allochrous* (fig. 7) has the largest chromosomes of any found in this study.

Section Collini (figs. 8–10, idiograms 8–10).—In contrast to the low correlation of chromosome morphology with geographical distribution in *A. stenophyllus* of section *Homalobi,* here there is much similarity in chromosome morphology from plants separated by even greater distances.

Section Hamosi (figs. 11–13, idiograms 11–13).—The two species with the 24 chromosomes, *A. arthurii* and *A. andersonii,* have little in common with the 26 chromosome species *A. congdonii.* The latter (fig. 13) has five pairs of "C"-shaped chromosomes, while the former two species have only two pairs. *Astragalus arthurii* is unique in that one chromosome (the last in idiogram 12) shows a prominent constriction at about the middle, which might be the centromere region. Chromosomal data beyond that now available should be obtained before a revision of the *Hamosi* is attempted.

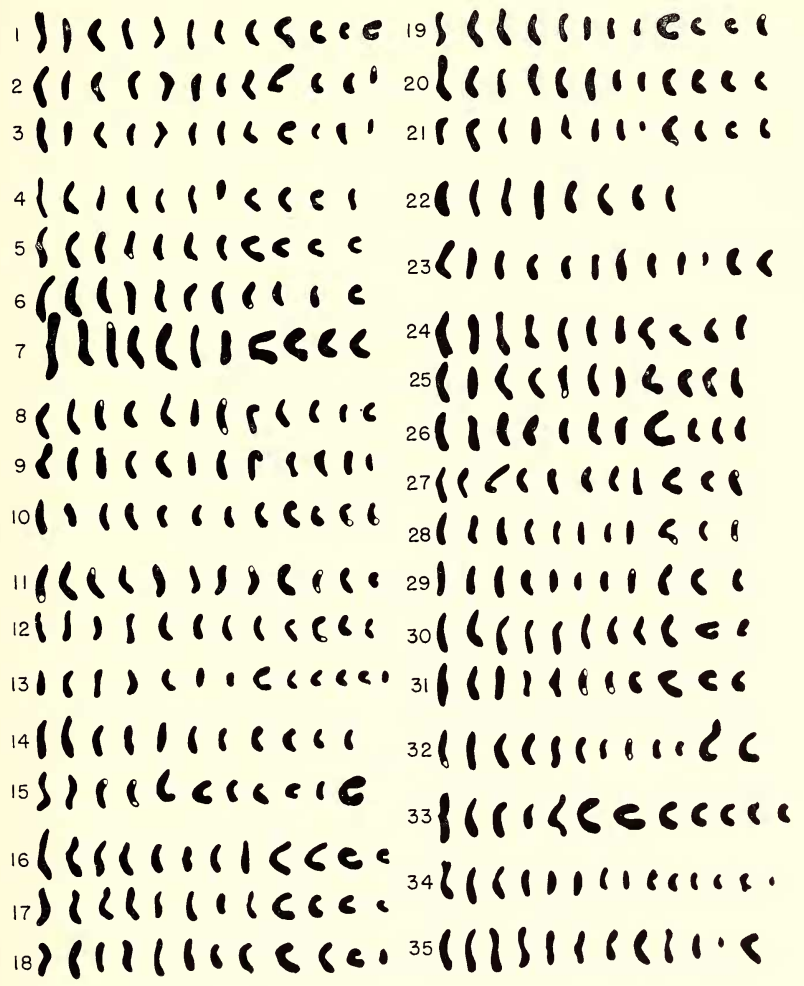
Section Podo-sclerocarpi (figs. 14–15, idiograms 14–15).—Vilkomerson studied nine species belonging here, including *A. sclerocarpus,* and found the same chromosome number (2n=22) in all. *A. pachypus* is the only new report for a species of this section. Unlike *A. sclerocarpus* (idiogram 14), *A. pachypus* (idiogram 15) has several pairs of "C"-shaped chromosomes.

Section Reventi-arrecti (figs. 16–21, idiograms 16–21).—Members of this section have very similar chromosomes. Each of the five species studied has four pairs of "C"-shaped chromosomes. Although these chromosomes vary somewhat in length they are otherwise very similar. *Astragalus eremeticus* var. *malheurensis* (idiogram 21) differs somewhat from the others by having a pair of small "dot" chromosomes not found elsewhere in this section.

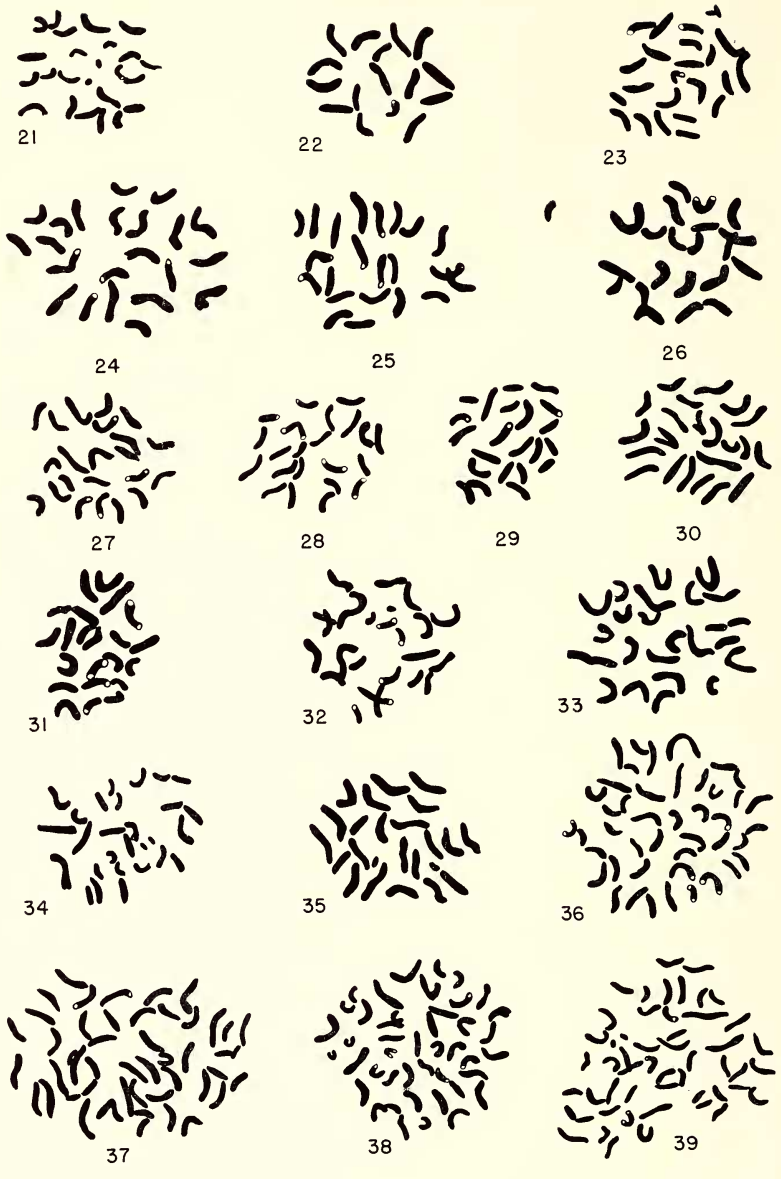
Section Uliginosi (fig. 22, idiogram 22).—Only one species of the *Uliginosi* has been studied, *A. canadensis* L., reported by Vilkomerson, and *A. canadensis* var. *mortonii* of this study.

Section Chaetodontes (fig. 23, idiogram 23).—*A. spaldingii* is the only member of this section thus far studied.

Section Argophylli (figs. 24–31, 38; idiograms 24–31).—The *Argophylli,* as a section, show a close likeness in chromosome morphology and number. This similarity is perhaps to be expected with closely related species such as *A. inflexus* and *A. purshii,* but it would not necessarily



Idiograms 1–35. Chromosomes of *Astragalus.* 1–3, *A. stenophyllus*; 4, *A. lentiginosus* var. *lentiginosus*; 5, *A. cusickii*; 6, *A. beckwithii* var. *weiserensis*; 7, *A. allochrous*; 8–9, *A. collinus* var. *collinus*; 10, *A. collinus* var. *laurentii*; 11, *A. andersonii*; 12, *A. arthurii*; 13, *A. congdonii*; 14, *A. sclerocarpus*; 15, *A. pachypus*; 16, *A. arrectus*; 17, *A. sheldonii*; 18–19, *A. riparius*; 20, *A. conjunctus*; 21, *A. eremeticus* var. *malheurensis*; 22, *A. canadensis* var. *mortonii*; 23, *A. spaldingii*; 24, *A. inflexus*; 25–28, *A. purshii* var. *glareosus*; 29, *A. purshii* var. *purshii*; 30, *A. chamaeleuce*; 31, *A. cibarius*; 32, *A. succumbens*; 33, *A. mollissimus* var. *earlei*; 34, *A. diaphanus*; 35, *A. gypsodes.* Camera lucida drawings, × 1450.



Figs. 21–39. Chromosomes of *Astragalus*. 21, *A. eremeticus* var. *malheurensis*; 22, *A. canadensis* var. *mortonii*; 23, *A. spaldingii*; 24, *A. inflexus*; 25–28, *A. purshii* var. *glareosus*; 29, *A. purshii* var. *purshii*; 30, *A. chamaeleuce*; 31, *A. cibarius*; 32, *A. succumbens*; 33, *A. mollissimus* var. *earlei*; 34, *A. diaphanus*; 35, *A. gypsodes*; 36, *A. cusickii*; 37, *A. collinus* var. *collinus*; 38, *A. purshii* var. *glareosus*; 39, *A. congdonii*. Camera lucida drawings, × 1450.

extend to such distant species as *A. chamaeleuce* from Colorado or to *A. cibarius* from southeastern Idaho. It would be interesting to determine if this similarity is maintained throughout this large section. *Astragalus cibarius* is excluded from the *Argophylli* by Barneby (1947), and he suggests a relationship with the *Malaci* for this species. On the basis of chromosome morphology and number, however, it seems very much like the other *Argophylli* and very little like the only representative of the *Malaci, A. succumbens,* thus far studied.

Section Malaci (fig. 32, idiogram 32).—*Astragalus succumbens* has one pair of large "C"-shaped chromosomes and a pair of "question mark"-shaped chromosomes.

Section Mollissimi (fig. 33, idiogram 33).—*Astragalus mollissimus* var. *earlei* has eight pairs of "C"-shaped chromosomes.

Section Sarcocarpi (fig. 35, idiogram 35).—*Astragalus gypsodes* has 11 pairs of relatively long chromosomes and 1 pair of very short ones.

Astragalus diaphanus (fig. 34, idiogram 34) has not been determined as to section. This species stands alone among the North American species studied in that the 2n chromosome number is 28. The chromosomes are also the smallest observed in this study. Jones (1923) listed *A. diaphanus* as a variety of *A. lentiginosus,* a member of his section *Inflati.* Barneby (1945) excluded *A. diaphanus* from his section *Diplocystium* (composed of the varieties of *A. lentiginosus*), but did not propose a new status. *A. diaphanus* should be excluded from the *Inflati* on the bases of chromosome number and fruit morphology. These reasons also support Barneby's exclusion of it from the *Diplocystium.*

Polysomatic Cells. In *Astragalus,* as in many other genera of the Leguminosae, both diploid and tetraploid cells may be found in the same root tip. Vilkomerson reported polysomaty in three species, but listed its occurrence as rare. Polysomatic cells were found by Tschechow (1930) in two of the species he studied. In one of these, *A. candidissimus,* tetraploid cells were found in forty per cent of the metaphase plates. Polysomatic cells were observed in four of the taxa of the present study: *A. cusickii, A. purshii* var. *glareosus, A. collinus* var. *collinus,* and *A. congdonii* (figures 36, 37, 38 and 39). In the last three species the occurrence of such cells are rare, but *A. cusickii* had about the same percentage of tetraploid cells found by Tschechow in *A. candidissimus.*

Summary

Mitotic chromosome studies were made of twenty-six species of *Astragalus* represented by thirty-five collections. The 2n chromosome numbers of 16, 22, 24, 26 and 28 were found. The basic number of 14 is added to those previously reported for the North American species. Chromosome numbers for species of the sections *Homalobi, Collini, Hamosi, Reventiarrecti, Argophylli, Chaetodontes, Malaci* and *Mollissimi* are reported for the first time. Counts for three species substantiate those previously published. Certain species and some sections of the genus can be readily rec-

ognized on the basis of chromosome morphology. *Astragalus diaphanus* should be excluded from the *Inflati* on the basis of chromosome number and morphology.

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INNOVATIONS IN DUDLEYA

Reid Moran

As a thesis at the University of California, I prepared a revision of *Dudleya* (Crassulaceae). This revision is not yet ready for publication and may not be ready for several years. Meanwhile, two floras including *Dudleya* are nearly completed, and there is immediate need for certain names from the thesis. Therefore, one new subspecies will be described and several new combinations proposed. Abbreviations for the names of herbaria are according to Lanjouw and Stafleu (1956).

Dudleya abramsii Rose subsp. **murina** (Eastwood) Moran, comb. nov. *Dudleya murina* Eastwood, Proc. Calif. Acad. IV. 20: 147. 1930.

Dudleya cymosa (Lemaire) Britton & Rose subsp. **gigantea** (Rose) Moran, comb. nov. *Dudleya gigantea* Rose in Britton & Rose, Bull. N.Y. Bot. Gard. 3: 23. 1903.

Dudleya cymosa (Lemaire) Britton & Rose subsp. **marcescens** Moran, subsp. nov. A subspeciebus ceteris caudicibus tenuioribus, rosulae